AN APPARATUS FOR OBSERVING THE TRANSPIRATION STREAM.

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(WITH TWO FIGURES)

THERE are, roughly speaking, two sets of experiments by means of which we can investigate the presence of the transpiration stream in small plants. One of these is concerned with the root of the plant and with the demonstration of the phenomenon known as root pressure. The other set deals with the shoot and the suction exerted by it on the water which is being absorbed by the root.

We all know what happens when we fix some kind of root pressure apparatus to the stump of a small plant, like a fuchsia for example. Water will soon be pressed out of the stump with sufficient force to raise a column of mercury to a considerable height. We can at the same time attach to the shoot of the very plant used for the root pressure experiment some form of potometer. We will observe suction and a column of mercury can be raised to a considerable height thereby. Do these two separate experiments really—even approximately—show what was going on in the plant at the time the experiment was set up? I think the answer must be no. When the plant in question was cut across, the stump exhibited the phenomenon of pressure, but the shoot that of suction at the same level. It is obviously impossible that pressure and suction should be exhibited by an intact plant at the same level. It must be mentioned here, however, that if the two experiments are set up very quickly, we may find the stump exhibiting suction for a short time. This changes to pressure when the stump is saturated with water. The root may of course become saturated in a few minutes by simply being exposed to water during the setting up of the experiment. We do not therefore get a clear idea of what is going on in the plant, when we isolate the shoot from the root, by attaching to each one a separate apparatus.

In order to learn more about the relation between shoot suction and root pressure it is obviously necessary not to separate the two portions of the plant entirely, but rather to keep them connected by some continuous bit of apparatus, so that, although the plant be cut in two, the shoot suction may still act on the root or the root pressure on the shoot. I use for this purpose a simple bit of glass apparatus, which I have called a *pinometer.* It will be necessary first to describe the apparatus; secondly, the way it is set up; and finally, to refer to a few of the experiments and the results obtained.

The pinometer consists of a straight bit of glass tubing (*fig. 1, b–d*), to which is obliquely attached by annealing on one side another short bit of glass tubing (*c–f*). On the opposite side a U-tube with an oblique connection is annealed on (*a–e.*) We have therefore four openings to this part of the apparatus (*a, b, c, d*). The bore of the glass tubing used for the pinometer depends entirely on the thickness of the stem of the plant used. The diameter of the glass tubes should about equal the diameter of the latter. A very convenient plant to use for demonstration purposes is a healthy fuchsia plant, not exceeding two feet in height.

The experiment should not be set up till all the various parts and tools are quite ready. The glass tubing should be cleaned to remove any greasiness, which is often the cause of introducing minute air bubbles into the system of tubes. The air should also be carefully removed from the rubber tubing. The more quickly everything is set up, the more nearly will the results obtained show what was going on in the plant at the time the experiment was made.

When everything is ready, the plant in its flowerpot is put into a bucket of water, so that it is immersed to a few inches above the point at which it is to be cut across. The leaves should not be moistened more than is absoluely necessary. The stem of the plant is now cut across under water in such a way that there is about one inch of stem, above and below the cut, devoid of buds or branches. If the stem has already a complete wood cylinder, the cortex may be removed with a sharp knife for about half an inch above the cut on the shoot, and below on the root.

The lower end of the shoot, without removal from the water, is fixed by rubber tubing to the opening *a, fig. 1,* and the portion *a–e* of the pinometer remains full of water, even when removed from the water, and can be temporarily held by a clamp (*i*) on a retort stand.[1] Next some rubber tubing is slipped over the upper end of the root stump. This bit of tubing also fills with water and the whole flowerpot can now be removed. The end *b* of the pinometer is now quickly fixed to the rubber tubing over the stump. A gauge is securely attached to *c*, and water is poured into *d* from a small reservoir (*fig. 3, r*) till the whole system of tubes is full of water. Mercury is then poured into the outer limb of the gauge, and this causes water to pour out at *d*, to which some pressure tubing has been firmly fixed. When there is enough mercury in the gauge to give the columns sufficient play to rise and fall, the opening at *d* should be closed by a pinch-cock and the experiment is set up. Retort stands and clamps are used for keeping the various parts in position, and a millimeter scale (*k*) can be attached to one or both limbs of the gauge.

Should air make its appearance, it will collect under *d*, if it comes from any part of the plant except the lower end of the shoot. It can be removed from *d* by opening the pinch-cock and allowing water to run in from the reservoir. Should it accumulate under *a*, the shoot must be removed from the rubber tubing attaching it to the glass, and water allowed to enter the pinometer at *d* rather slowly. It will then be running out slowly at *a*, and the shoot is again fixed, the current of water preventing any air getting in.

In any case the removal of air means the opening of the pinch-cock at *d*, and this causes the mercury to go back to its starting point. This can be obviated by inserting a stop-cock between the oblique bit *f–c* (*fig. 1*) and the gauge. I do not however consider this necessary for the apparatus, which as described here is intended chiefly for qualitative and not quantitative observations.

The results obtained with the pinometer depend very much on the point at which we fix it in the plant. I will refer therefore to a few actual experiments, which I hope will show the value, however small, of the simple bit of apparatus just described.

In the first experiment to be described, a pinometer was fixed to

[1] For fixing the plant to the glass tube it is best, if possible, to employ some kind of pressure tubing. The latter can be made secure by tying with string or by employing some kind of clamp. The use of wire is to be deprecated.

the main shoot by cutting the stem a short distance above the lowest lateral shoot (*fig. 1*). After a very short time the mercury in the limb (*g*) of the gauge nearest the plant was seen to rise, as the latter was withdrawing water from the pinometer. As the mercury rises, the pull on the lower end of the shoot and on the upper end of the

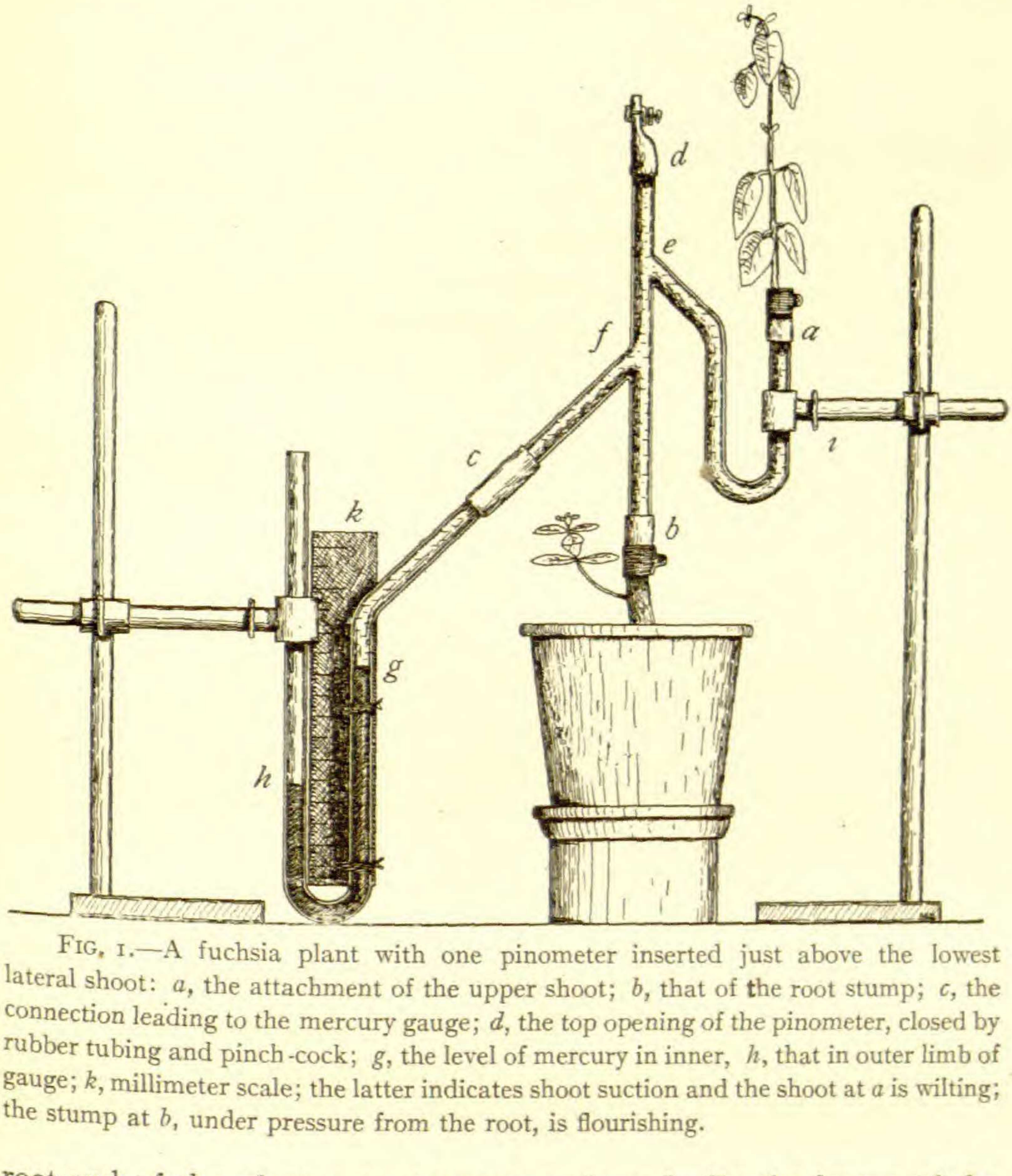

FIG. 1.—A fuchsia plant with one pinometer inserted just above the lowest lateral shoot: *a*, the attachment of the upper shoot; *b*, that of the root stump; *c*, the connection leading to the mercury gauge; *d*, the top opening of the pinometer, closed by rubber tubing and pinch-cock; *g*, the level of mercury in inner, *h*, that in outer limb of gauge; *k*, millimeter scale; the latter indicates shoot suction and the shoot at *a* is wilting; the stump at *b*, under pressure from the root, is flourishing.

root-end of the plant gets stronger, and gradually the leaves of the upper shoot wither. It will be noticed that the leaves of the lowest lateral shoot are quite fresh. Before the upper shoot dies altogether its axillary buds will generally develop and form small leaves, but even these succumb in the end.

In this experiment, therefore, and at the height in question, our plant exhibited shoot suction when tested by the pinometer. A modified barograph recording cylinder, made by NEGRETTI & ZAMBRA, was arranged to record the rise of the mercury in this particular experiment. A burette-float was placed on the mercury in the open end of the gauge (*h*). It was suspended by a fine thread, which ran over a pulley and was attached on the other side to the free end of a lever, the other end of which carried a pen which wrote on the revolving cylinder. The records taken during the first week showed that the water taken in from midday to midnight and that taken in from midnight to midday was in the proportion of three to two. Never did any pressure from the root, during night or day, cause the amount of water taken in to fall below nought.

In a second experiment a pinometer was fixed into a fuchsia plant about one inch above the soil and quite below the lowest lateral shoot. Root pressure manifested itself very soon and the mercury was forced out of the inner limb of the gauge, rising of course as rapidly in the outer one. In this case there was obviously pressure on the cut surfaces of shoot and root. The leaves of the shoot kept fresh as long as the pressure lasted, which was for sixteen days. On the sixteenth day there was a difference in the level of the mercury in the two limbs of the gauge of 20^{mm}. Allowance however must be made for the column of water resting on the mercury in the inner limb of the gauge. After the sixteenth day the pressure was gradually reduced, very probably owing to the root becoming exhausted, its supply of organic food from the green leaves being cut off. The leaves began to wither as the pressure of the root decreased.

In a third experiment two pinometers were employed (*fig. 2*). One was fixed to the fuchsia plant just above the soil and the other just above the lowest lateral shoot. The plant was therefore cut into three parts, the lowest one of which, the stump, was devoid of any lateral shoots. The gauge attached to the lower pinometer (P_1) very soon indicated pressure from the root, that of the upper pinometer (P_2) suction from the two portions of the shoot. We have therefore in this experiment an arrangement by which root pressure and shoot suction can be observed at the same time. The difference in the appearance of the leaves on the two portions of the shoot is very striking. The leaves of the upper shoot are dead, there being a strong pull on the lower end. The leaves of the middle shoot are flourishing, there being a push on its lower end, although the lower pinometer is separated from the upper one by about two inches of stem only

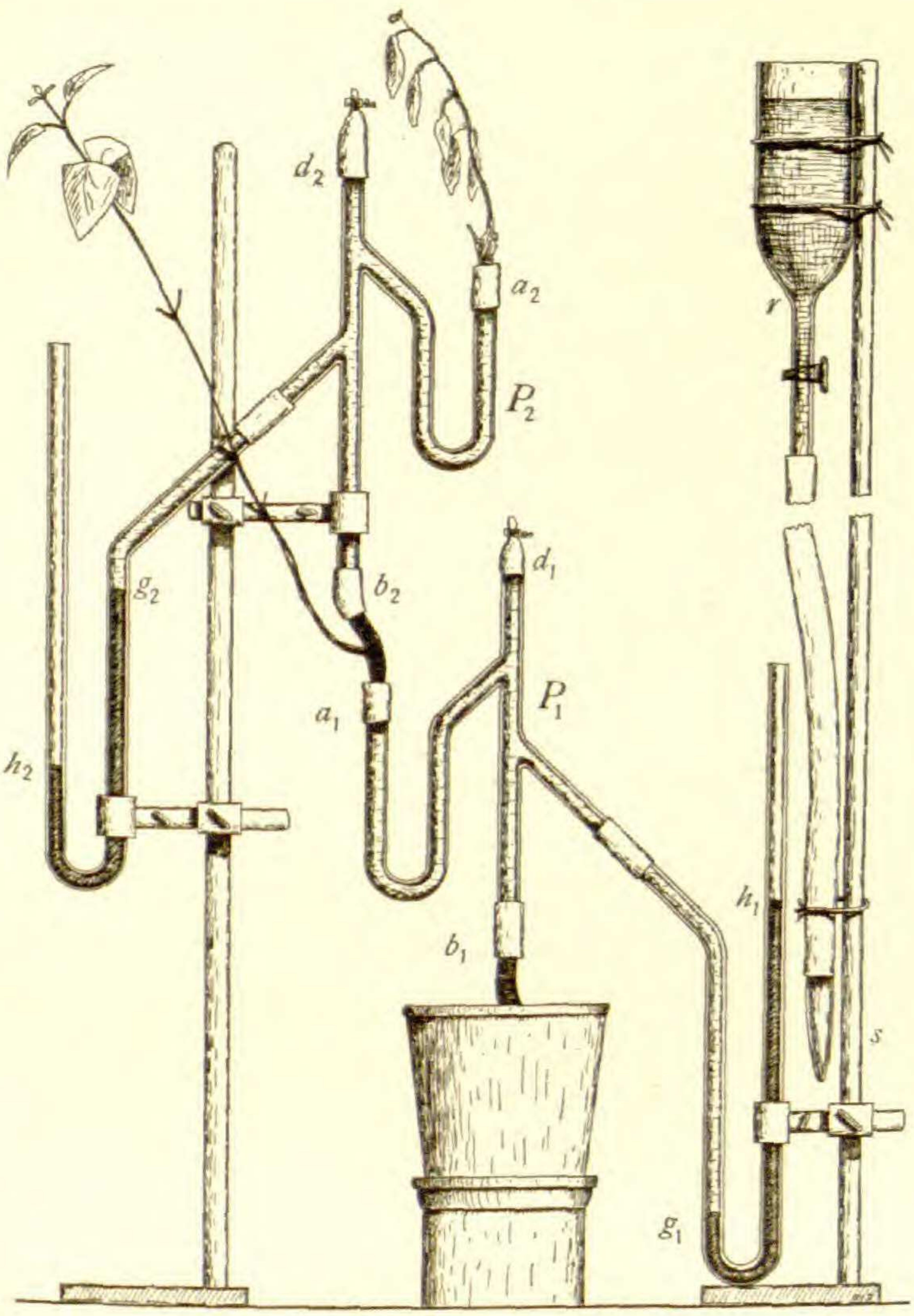

FIG. 2.—A fuchsia plant with two pinometers: the lettering as in *fig. 1;* the lower pinometer (P_1) shows root pressure and its shoot (a_1) is flourishing; the upper one (P_2) exhibits shoot suction, and its shoot (a_2) is wilting; *r*, reservoir of water, *s*, its spout.

(between a_1 and b_2). A fortnight after being set up, a reading for this experiment showed a difference in level of the two columns of mercury of 18^{mm} in the lower pinometer, indicating pressure from the root, and a difference of 20^{mm} in the upper pinometer, indicating suction from the shoot.

An experiment was also made with three pinometers inserted into the stem of a fuchsia plant. The following readings were taken after the experiment had been going on for some time. The lower pinometer showed root pressure with a difference in the level of the mercury columns of 31^{mm}, the middle pinometer showed suction with a difference in level of 85^{mm}, and the upper pinometer suction with a difference of 63.5^{mm}. The figures for the next day in millimeters were 39 (an increase of 8), 127.2 (42.2), and 128 (64.5) respectively. The two lower pinometers were below the lowest branches. In this case, therefore, root pressure could not be observed even up to the lowest lateral shoot. As in all the previous experiments, suction, where observed at all, was maintained day and night, till, owing to the pull on the cut surface of the plant, air made its appearance and the mercury returned to its original level.

The pinometer, as described here, is meant to be of use chiefly for class and demonstration purposes. I wish now to point out what the results obtained by employing it are, that is to say what observations can be made on the transpiration stream.

We can readily see that in our plants, at least, it is never a function of the root to press water up into the leaves. By day and by night the phenomenon of root pressure can be observed only below the lowest shoot. But root pressure is an extremely useful if not a necessary process by which the rise of the water is started. Referring to those of our experiments in which the lower cut surface of the shoot was exposed to pressure, we see that the plants do not suffer much by the stem being cut across. It appears to be necessary that water should be forced into the lowest end of the vascular system; or at least there should be no pull on it. Root pressure, therefore, is not only a symptom of the avidity with which the roots are absorbing water, but it is of importance as assisting in the starting of the transpiration current.

It must be mentioned here, however, that the insertion of a pinometer into a fuchsia plant is in any case a serious thing for the latter. The phenomena of exudation and bleeding seem to cease entirely when the shoot has been severed from its connection with the root. This statement holds good whether the gauge of the pinometer shows pressure or suction. The fact that at different heights in the plant we get readings which at least show that the pressure may vary very much in even two or three inches of stem, is a proof, I think, that the "atmospheric pressure" theory of the rise of water is not correct.

When we get away from the root we find the phenomenon of shoot suction manifesting itself. In fact, as already pointed out, shoot suction generally seems to be stronger than the pressure from the root at any point except just above the root. That is to say, the shoot is able at any time to take in more water than can be supplied by the root. Numerous experiments show that this is the case in winter and summer, day and night, in the plants I experimented upon.

Which part of the plant is exerting this suction? I have spoken here of shoot suction, but it is possible to split up this part of the transpiration stream into two distinct processes, namely the leaf suction and the wood lift. There is not much mystery about the former. We can understand how the water is removed from the finest endings of the vascular system. If, however, we remove the leaves from a shoot which has been attached to a pinometer or even cut off the upper part bearing leaves, leaving only a short leafless shoot stump, we still get water rising in the wood and exerting a pull on the gauge of the pinometer. The activity of the leaves simply removes the water from the top of the vascular system, and this water is replaced by a process going on in the wood.

I am mentioning this simply to show that in the experiments with the pinometer the taking in of water by the shoot is not a phenomenon of leaf suction but one of wood lift. The force of the wood lift is very great; it is generally greater than the root push. But, as our experiments show, it cannot act efficiently for any length of time if the lowest end of the vascular system is exposed to a pull from below. It is as yet not known how the wood lift acts. It is therefore all the more necessary to make as many observations as possible on this process. I think the pinometer does make it possible to observe at least one property of this water current. It is continually in a state of what is known as "negative pressure." A natural result of this is that the air, which the water absorbed by the plant contains under ordinary atmospheric pressure conditions, escapes from the water when inside the plant. Over and over again my experiments have been brought to an end by air collecting, generally under the shoot. Air-bubbles are bad for the conducting of the experiments, and the more they are kept out the more water is absorbed by the plant when attached to a pinometer. It is obvious that the plant must also guard against the accumulation of air in the column of water which fills the vascular system. No doubt this will in part account for the peculiar structure of the wood elements. Do the latter bear any relation in their structure to the nature of the water generally found in the localities in which the plant grows?

The form of pinometer mentioned in this paper is intended, as already mentioned, essentially for demonstration purposes. It is possible by its use to observe, more clearly than hitherto, the relation between shoot suction and root pressure. Owing to the preliminary nature of this paper I have refrained from giving any lengthy readings taken during the experiments. Their value in any case would not be very great, being taken with the simple form of pinometer here described. A more elaborate bit of apparatus is therefore in course of construction, by which any air making its appearance in any part of the pinometer is removed automatically at regular intervals without altering the conditions of pressure inside the system of tubes. Furthermore, it is connected with an automatic recording instrument, in which the difference in the height of the two mercury columns will be reduced as much as possible.

The nature of this paper, I hope, will excuse my having made no reference to any literature. It was not my intention to discuss the old or bring forward a new theory with regard to the rise of water. We still have the suction by the leaves, the pressure by the root, and the as yet little understood lifting of the water by the wood. In writing this paper, it was my object to give an account of a very simple bit of apparatus. by means of which various phenomena connected with the transpiration stream in small plants could be readily observed. I hope later on to be able to publish some more detailed observations on the properties of the wood lift, taken by more elaborate instruments.

Diagrams illustrating the working of the pinometer were shown at the last Cambridge meeting of the British Association.

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